Timing of aggregation and larval release by Tanner crabs, *Chionoecetes bairdi*, in relation to tidal current patterns

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Abstract

Each spring, female Tanner crabs, *Chionoecetes bairdi*, form high density aggregations at 150 m depth in Chiniak Bay, Kodiak, AK. Within the aggregation, crabs form mounds containing hundreds to thousands of animals. In 1991, over 200 mounds and 100,000 crabs were present in an area of about 2 ha. Previous studies have suggested that aggregation and mating are synchronised with spring tidal cycles. In 1999, we placed a current meter near the aggregation, then observed aggregation behaviour with a video camera sled and remotely operated vehicle (ROV) over an 8-week period. Crabs were collected from the aggregation with the ROV, brought into the laboratory, and the numbers of hatching larvae were determined daily. Mound formation began in mid-April, hatching began around 7 May, and the median hatch date coincided with the strongest tides on 17 May. During this time, net tidal flow reversed for 3–4 days. In the laboratory, individual crabs released an average of 129,400 larvae over a period of 9.4 days. Over 74% of larvae hatched between 2000 and 2400 h. These data suggest that larval hatching is optimised to take advantage of tidal current patterns. It also implies that the timing of larval hatching for *C. bairdi* changes in monthly steps, and is decoupled from planktonic food production.
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Keywords: Chionoecetes bairdi; Aggregation; Behaviour; Crab; Hatching; Larvae; Tides

1. Introduction

The Tanner crab *Chionoecetes bairdi* and snow crab *Chionoecetes opilio* have historically supported valuable commercial fisheries in Alaskan waters. Combined value of the Bering Sea fisheries for these two species exceeded US$ 400 million in 1991 (ADF&G, 1999). However, both snow and Tanner crab populations undergo large-scale swings in abundance. Snow crab landings have fluctuated from 143,000 t in 1991 to 11,000 t in 2000. Tanner crab abundance is so low that fisheries have been closed in the Bering Sea since 1996 and in the Gulf of Alaska since 1994. Biological knowledge of these species is too poor to dis-

tinguish whether crab population cycles result from environmental change, inherent factors (e.g. density dependence) or fishery effects. Environmental change could affect abundance by altering the time at which crab larvae hatch, or the abundance of planktonic food sources at the time of hatching. The match–mismatch hypothesis (Hjort, 1914; Cushing, 1990) suggests that survival of larvae will be high when hatching occurs coincident with the presence of optimal feeding conditions, and poor when these events do not coincide.

During the past 30 years, large-scale changes have occurred in the climatic, oceanographic, physical and biological characteristics of the North Pacific Ocean (Royer, 1989; Trenberth and Hurrell, 1995; Francis et al., 1998); these are now dubbed the Pacific decadal oscillation (PDO). The most notable change in the Gulf of Alaska occurred in 1977 and resulted in a

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major increase in temperature, subsequent precipitous declines in abundance of crab, shrimp and small pelagic fish, and increases in salmon, gadids and flatfishes (Anderson et al., 1997; Francis et al., 1998; Anderson and Piatt, 1999). However, swings in snow and Tanner crab abundance are out of synchrony with the PDO. Sainte-Marie et al. (1996) suggested that abundance cycles may be an inherent feature of snow crab populations, resulting from a combination of ontogenetic changes in fecundity and sex ratios, and cannibalism by older year classes on recruiting cohorts.

Some marine species such as sea urchins have adapted to environmental variability by evolving mechanisms coupling larval release to phytoplankton abundance (Starr et al., 1990). Most crab species, on the other hand, time their spawning to coincide with local tidal cycles, allowing them to take advantage of water currents and density structures to deliver larvae to the appropriate environments (Morgan, 1995; Morgan and Christy, 1995). Concurrently, crab larvae have evolved vertical migratory patterns that take advantage of such tidal patterns. Starr et al. (1994) found that mature female snow crab released larvae shortly after exposure to senescent phytoplankton, and concluded that the crabs utilised this signal to stimulate larval release at a time when zooplankton abundance would be optimal. However, they did not account for entrainment to local tidal conditions, which may be equally or more important. In fact their crabs released larvae coincident with local high spring tide. Moulting (and subsequent mating?) of adult female *Carcinus maenus* occurs coincident with expected high tides (Abello et al., 1997), even after being in the laboratory for some time, suggesting that they have a biological clock which is periodically reinforced by tidal signals.

Many species of crabs release larvae synchronous with high tides, often at night, but occasionally during daytime (Forward, 1987; Morgan, 1987; De Vries and Forward, 1989; Saigusa, 1992; Morgan and Christy, 1995; Palmer, 1997; Amend and Shanks, 1999; Saigusa, 2000; Yamaguchi, 2001). Most species studied, however, have been intertidal, estuarine, or subtropical. Understanding the factors that control timing of larval release would provide better insight into how crab larvae survive their critical early life stages, and how environmental variability or change affects recruitment and production of crab populations.

In 1991, using the two-person submersible Delta, we discovered that female Tanner crab formed a dense aggregation in 150 m of water in Chiniak Bay, Kodiak, AK, during the spring mating season (Stevens et al., 1993, 1994). Within the aggregation, females formed mounds containing 100–400 crabs, spaced at intervals of 1–3 m. Males were present around the perimeter, and between mounds, where they mated with individual females. The entire aggregation contained over 100,000 crabs in an area of about 2.2 ha. Subsequent studies conducted in 1992, 1994 and 1995, using the Delta and a remotely operated vehicle (ROV) revealed that only mature females with eyed (pre-hatching) embryos were present in the mounds, and their reproductive conditions (weight of spermathecal contents and gonadosomatic index) were essentially homogeneous (Stevens et al., 1996). Hypothetical explanations for aggregation and mound formation (Stevens et al., 1994) included the possibility that mounds functioned as pheromone towers to attract males, that mounds might limit access by males to females that were not ready for re-mating and that it was associated with larval release.

Careful review of data collected over 5 years of observation (1991–1995) showed that the timing of aggregation varied annually, and suggested that mound formation was associated with larval release, coincident with the onset of high spring tides in April or May, but not with changes in temperature, the full moon or phytoplankton indices (Stevens et al., 2000). Each of our previous three hypotheses was examined for consistency with these data. Counts of crabs made by ROV or submersible in 1995 did not show a sharp increase in male abundance, which would be expected if mounds functioned primarily to attract males. Homogeneous reproductive conditions of females did not support the idea that crabs in mounds were more reproductively ready than non-mounded crabs. The data did support the hypothesis that mound formation was associated with larval release, and might be a mechanism for improving larval survival, perhaps by elevating them above the surrounding silty mud. This "larval launch pad" hypothesis (Stevens et al., 2000) has the following testable predictions:

(1) mound formation occurs coincident with local high spring tides;

(2) local tides produce detectable changes in current patterns at the depths where the crabs occur (150 m);

(3) mounds are associated with synchronous larval release;

(4) female crabs would form mounds when they were ready to release larvae, and would leave the mounds immediately after hatching was completed.

Starting in 1999, we began testing this hypothesis using video camera sleds and ROVs to monitor the length of the mounding process and to determine its relationship to hatching.

2. Materials and methods

2.1. Environmental observations

Water clarity was recorded daily with a 20 cm Secchi disk, by measuring the depth at which it was no longer visible, in 0.25 m increments. It was not possible to make daily boat trips 16 km out to the site of crab aggregation in Chiniak Bay, so observations were made from a dock in Trident Basin, an arm of Chiniak Bay, in 20 m water depth, approximately 50 m from the water intake to the Kodiak Fisheries Research Center (KFRC). Current speed and direction, and water temperature and salinity were measured at 2 h intervals in Chiniak Bay by an instrument array on a subsurface mooring at 192 m depth (6 m above bottom in 198 m of water). The mooring was deployed on 12 April 1999, with the assistance of the NOAA Pacific Marine Environmental Laboratory (PMEL), at a position of 57° 43.2′ N, 152° 17.4′ W, approximately 500 m from the site of the crab aggregation, so as not to interfere with sled or ROV operations. Tide stage and height, and lunar phase were recorded from prediction tables. Tide exchange was calculated as the difference between the highest and lowest tides (which usually followed immediately) on each day.

2.2. Underwater observations

Initial observations were made with a towed video camera sled (the BRAD: Benthic Resource Assessment Device) using a black and white camera, 50 W light and a Hi-8 camcorder in a pressure housing.

Video could not be observed in real time because there was no electronic cable to the surface. The sled was towed from a chartered 17 m fishing boat along transects of 2–3 km length in Chiniak Bay, at depths from 125 to 200 m. Two to four transects were made each day at intervals of 3–4 days, weather permitting. Sled tows were made on 8, 9, 13, 14, 20 and 21 April 1999. Boat positions were logged using a military GPS receiver, with a precision of ±5 m. Positional lag of the sled was estimated from the water depth and towrope length. Upon return to shore, videotapes were reviewed, and time codes were assigned to each crab observed, using a commercial computer program ("The Observer", Noldus Corporation, The Netherlands).[1] A GIS program was used to plot numbers of crabs per 5 min interval (CP5M) taking into account the estimated lag behind the boat.

After crab mounds were observed with the sled, observations were made with a Phantom HD2 ROV (Deep Ocean Engineering Inc.) carrying a colour camera and Tritech 325 kHz sonar[1]. A heavy weight was suspended from the boat by nylon rope, and the umbilicus of the ROV was clipped to it as the weight and ROV were lowered together. The ROV had approximately 100 m of free tether from the weight. The sonar was used to locate the crab aggregation, and the ROV and boat moved into position for observation. Observations usually consisted of estimating the overall area of the aggregation from the sonar image, "flying" over the aggregation with the ROV to estimate the average size and distance between crab mounds, and then setting the ROV down next to a mound to observe crab activity. Observations continued for as long as possible (generally a few minutes to an hour), but were usually interrupted when silt obscured the picture or the boat and ROV drifted away. It was usually not possible to estimate numbers of crabs or size of mounds in a quantitative manner from ROV observations due to their erratic nature, but a subjective index of aggregation "intensity" was estimated on a relative scale from 1 to 10 on each date of observation. On some days, the ROV was towed from the weight with a bridle, or was flown behind it over a long straight line. On those occasions, crabs were counted in 5 min intervals like sled tows.

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[1] Reference to trade names does not constitute endorsement by the National Marine Fisheries Service.

On three occasions, a small net with 50 mm mesh was tied to the ROV frame beneath the camera and used to collect crabs from mounds, by flying the ROV into the mound, and skimming crabs off the top. Crabs were returned to the laboratory within 2 h for examination and observation.

2.3. Laboratory observations

Laboratory observations were made to address four questions: (1) What is the time span over which larval hatching occurs for an individual female? (2) What is the median hatching date for a group of crabs? (3) Is the hatching schedule affected by immersion in filtered versus unfiltered seawater, i.e. do the contents of natural seawater (e.g. phytoplankton) affect hatch timing? (4) At what time of day do larvae hatch?

Female crabs were collected by trawl from Kazakoff Bay on Afognak Island, approximately 50 km from Kodiak, on 4 April 1999, during a routine survey by the Alaska Department of Fish and Game (ADF&G) R/V Resolution, and transferred to tanks in the KFRC on 6 April. On that date, 12 crabs were placed into individual plastic aquaria filled with 10 l of filtered seawater, and designated as group F. All 12 aquaria were placed in a larger outer tank with running filtered seawater for temperature control. Twelve more crabs were placed in aquaria filled with raw, unfiltered seawater (group R). On 27 April, five female crabs were collected from mounds in Chiniak Bay with the ROV, placed in similar 10 l aquaria with unfiltered seawater, and designated as group C. Seven more female crabs were collected on 30 April, and added to group C. Aquaria were checked daily, and larvae counted as for groups F and R. A third collection of 34 female crabs was made at 0200 h on the morning of 21 May. These crabs were examined, and monitored daily to determine when extrusion of new clutches occurred, but larvae were not counted. Prior to placement in tanks, carapace width (CW) of each crab was measured across the widest part of the carapace, between spines, and shell condition was recorded on a five-point scale (Stevens et al., 1993).

Each aquarium was examined daily for the presence of larvae, and each crab was transferred to a tank with fresh filtered or raw seawater, according to its group designation. When fewer than 2000 larvae were present, all were usually counted. When larvae were more abundant, they were subsampled after water was added to each aquarium to bring the volume up to a pre-measured level of 12 l. Then, the water in the tank was stirred vigorously for 5 s, after which a subsample was obtained by dipping a 100 ml flask into the centre of the aquarium. Stirring was repeated before each subsample. Experimental subsampling with 10 crabs showed that the coefficient of variation (CV) declined from 25.6% with four subsamples of 100 ml, to 9% with eight subsamples. This was considered to provide adequate precision for a reasonable amount of effort, and all further estimates were made using eight subsamples. Larvae were counted by suctioning them into the large end of a 3 ml plastic pipette, holding them up to a light, and tallying with a thumb counter. Subsample counts were then averaged, and multiplied by the subsampling factor (120) to estimate the total number of larvae present. After each crab had released all her larvae and extruded a new clutch, it was transferred to a communal holding tank. Water temperature was monitored daily in one aquarium of each group of crabs with a digital logger. Mean CW, extrusion date and number of larvae hatched were compared by ANOVA and post-hoc comparisons were made with Tukey's HSD test. Non-parametric rank tests (Mann–Whitney or Kruskal–Wallis) were used to compare integer-scale variables including shell condition and the number of days on which 10 or more larvae were released. Numbers of larvae released were regressed against CW within shell condition categories. Crabs with a shell condition 3 were considered to be primiparous, i.e. carrying (and releasing) their first clutch of larvae, whereas those with shell condition 4 were considered to be multiparous, carrying their second or later clutch. Regression equations were used to predict the fecundity of each crab, according to its shell condition and size.

Seventeen female Tanner crabs were collected with the ROV on 28 April and 4 May 2000. Nine of these crabs were held in a group tank (group G), and eight were held in separate (group S) 10 l tanks. Fifty-two crabs captured in April 1999 had been divided into two groups of 26 crabs and held communally in either raw (group R) or filtered (group F) seawater. Hatched larvae were collected daily from each group in a net placed beneath the overflow drain. Larvae were concentrated on filter paper, rinsed with 100 ml each of seawater and freshwater, then dried to constant weight

at 60 °C, and weighed. Each day, three blank filter paper disks were rinsed in a similar fashion, then dried, and their mean weight subtracted from the dry weights of filters with larvae. Three additional crabs were held in separate 10 l tanks with filtered seawater, and their larvae were collected and water was changed every 4 h for 3 days during the period from 6 to 8 May 2000.

3. Results

3.1. Environmental information

Secchi disk readings varied daily about a mean of 7.5 m in early March 1999, then declined sharply from 12 to 20 March, to a new mean of 4.8 m (Fig. 1A), which lasted until September (not shown). This decline indicated the beginning of the plankton bloom in nearshore waters. Tidal exchange and percent lunation are shown in Fig. 1B. Currents on the bottom of Chiniak Bay are strongly tidal, with speeds from 3 to 10 cm/s, switching from north westerly on flood tides, to south easterly on ebb tides (Fig. 2). Af-

ter filtering with a 30 h low-pass filter, the long-term mean current was about 3 cm/s to the S.E. However, the mean current reversed to the NW for several days coincident with the highest spring tide (HST) of the month, around 18 April and 16 May 1999. In June 1999, these reversals began to occur on both weak and strong spring tides, and in July, a longer term reversal started on the HST and continued for several weeks. Water temperature at 192 m rose steadily from 3.37 °C on 12 April to 8.17 °C on 17 August (Fig. 3). Salinity declined from 32.6 to 31.8 ppt during the same time period.

3.2. Field observations

Dates of sled tows and ROV dives are shown in Fig. 4A, along with subjective indices of crab abundance. Only the highest number of CP5M observed on each day are shown. CP5M values >100 (log values >2) indicate that mounds were observed during the 5 min interval. Crab mounds were detectable from >50 m distance with the sonar on the ROV. Mounds were first observed on 13 April 1999, about 1 month
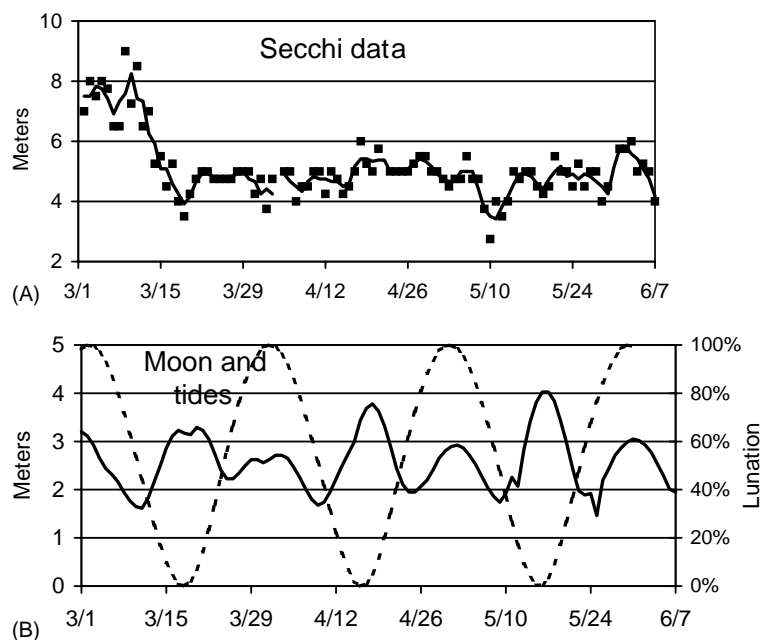

Fig. 1. (A) Secchi disk depth (m) at a dock in Trident Basin (squares) and the 3-day running mean (solid line). Note the strong decrease in Secchi depth in mid-March, signifying the beginning of the inshore spring plankton bloom. (B) Tide exchange (solid line) and phase of the moon (% lunation, dashed line) in March, April and May 1999. The strongest tides (greatest exchange) occurred during the new moon.
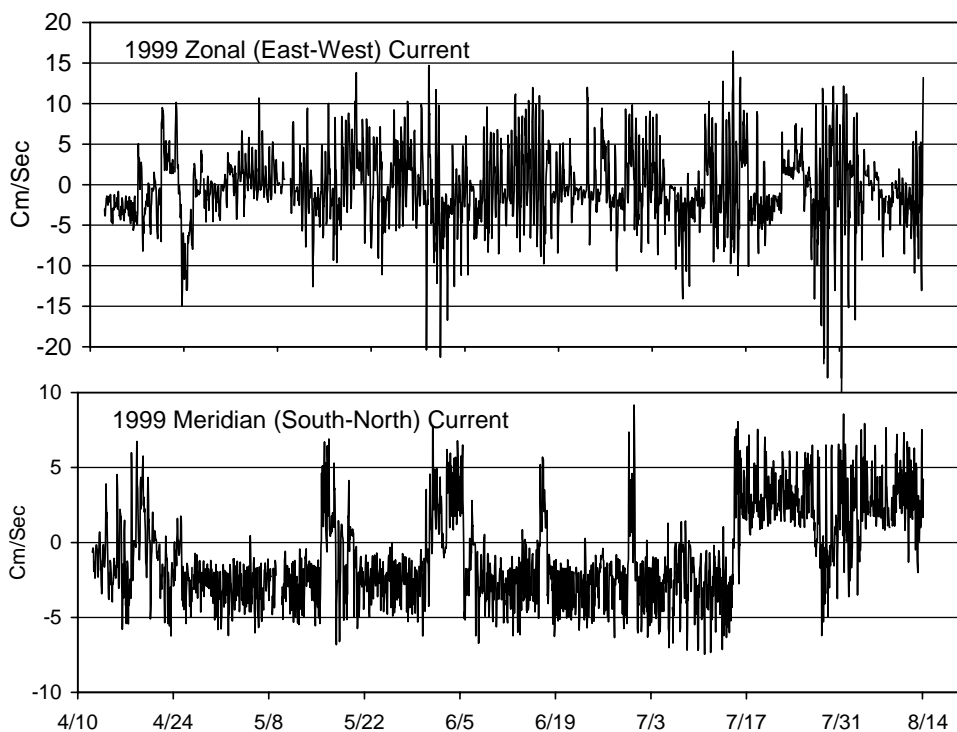
Fig. 2. Currents at 192 m depth (6 m off bottom) in Chiniak Bay, spring 1999. Top: zonal currents (east is positive, west is negative). Bottom: meridional currents (north is positive, south is negative). Data have been filtered with a 30 h low-pass filter. Mean current was about 3 cm to the S.E., except on spring tides, when it switches to the NW, as it did on 18 April, 16 May and 3 June. After 15 July, mean current was to the NW.
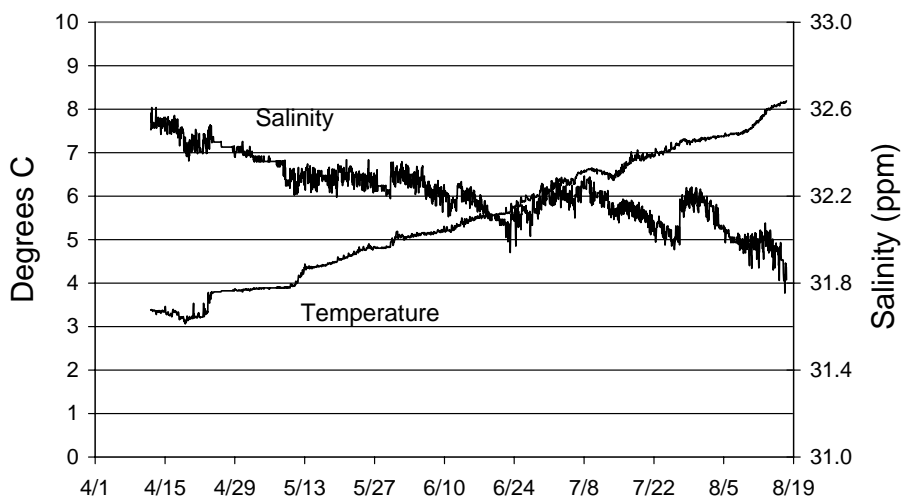

Fig. 3. Temperature (°C) and salinity (ppm) at 192 m depth in Chiniak Bay, spring and summer of 1999.
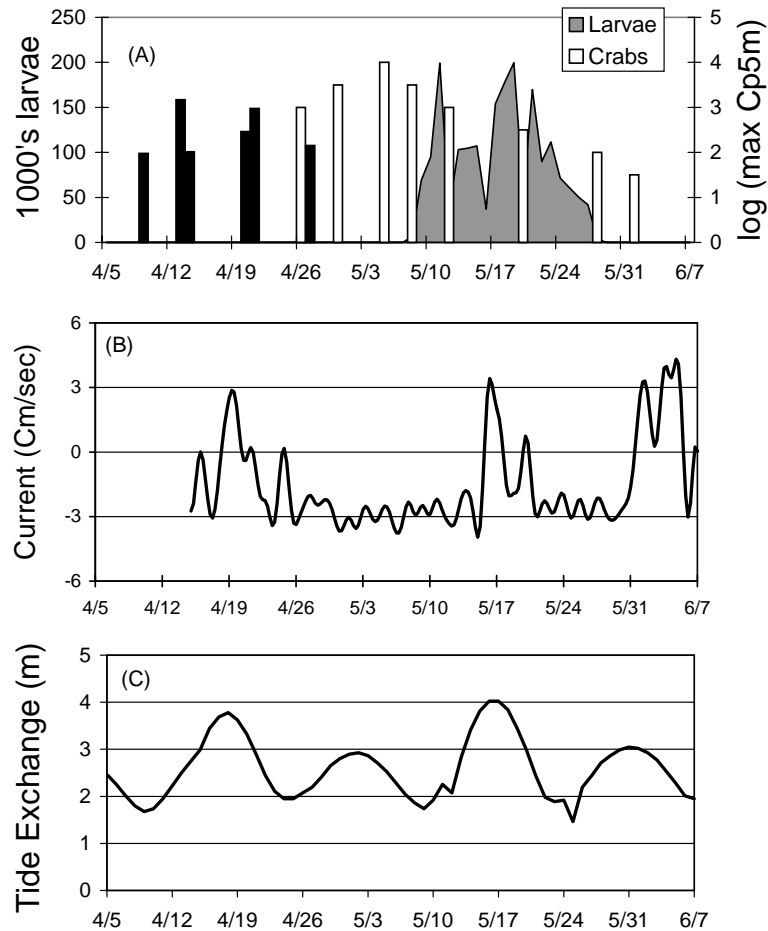
Fig. 4. (A) Indices of female Tanner crab abundance on dates observed in 1999. Black bars are the (log transformed) highest count of crabs in 5 min intervals (CP5M) on each day. White bars are relative estimates based on number and size of mounds observed. Shaded area represents numbers of crab larvae released daily by crabs in group C (Chiniak Bay). (B) Meridional (N–S) current speed at 192 m depth. Note correspondence of hatching with tides and currents on 17 May 1999. (C) Tidal exchange (difference between highest and lowest tides of the day).

after the spring plankton bloom, and lasted until 1 June. The greatest intensity of aggregation occurred up to a week before larval release began in the laboratory, and declined during the period of larval release, probably as crabs left the mounds after spawning. Larger mounds were observed in 1999 than in any previous year, some containing thousands of crabs. The largest was >5 m long × 1 m high and wide, with "peaks" exceeding 1.5 m at each end, and probably contained about 5000 crabs. With the ROV, we observed crabs climbing up one vertically faced mound until it overhung and broke loose, spilling crabs down the slope.

Among the 34 crabs captured on 21 May, 76% carried eyed, pre-hatching embryos, 15% were in the process of hatching, and <10% had completed hatching and begun extrusion of newly fertilised embryo clutches.

3.3. Laboratory observations of hatching

The 36 experimental crabs had a mean CW of 89.3± 6.8 mm, and shell condition of 3.8 ± 0.4; differences between groups were not significant for these factors (Table 1). Crabs started releasing larvae in small numbers for a few days and then larval release rapidly

Table 1
Comparative hatching data for three groups of female Tanner crabs, *C. bairdi*, in 1999[a]

	Group F	Group R	Group C	Mean (S.D.)	*F*-value	*P*-value
Origin (Bay)	Kazakoff	Kazakoff	Chiniak			
Capture dates	4 April	4 April	27–30 April			
Seawater type	Filtered	Raw	Raw			
Shell condition	3.6	3.8	3.9	3.8 (0.4)	3.457[b]	0.178
CW (mm)	88.1	87.7	92.1	89.3 (6.8)	1.607	0.216
Temperature (°C)	5.3	5.1	6.3	–	–	–
Mean number of larvae hatched	89396	137139	161900	129314 (53431)	8.163	0.001
Predicted hatch	110460	130417	165900			
Maximum number of hatched	184512	225617	209354	225617		
Maximum daily hatch	94215	106395	104895	106395		
Minimum number of hatched	13976	78161	59997	13976		
Days >9 larvae	11.9	9.8	6.6	9.4 (3.7)	17.031[b]	<0.001
Maximum hatching days	22	13	8	22		
Minimum hatching days	6	6	5	5		
Median hatch date	15 May	14 May	18 May	16 May	2.165[b]	0.339
Mean extrusion date	19 May	17 May	20 May	18 May	2.000[b]	0.368

[a] Crabs from Kazakoff Bay were captured by trawl, whereas those from Chiniak Bay were captured with the ROV. *F*- and *P*-values are from ANOVA comparisons.

[b] Denotes χ^2 value from Kruskal–Wallis test.

increased. Crabs captured by trawl on 6 April 1999 began hatching on 22 April, but none released >10 larvae until 1 May (Fig. 5). Crabs captured by the ROV on 27 and 30 April 1999 (group C) began releasing small numbers of larvae within a day of capture, and the first crab released 10 larvae on 7 May, 9 days after capture. Excluding the days on which <10 larvae were released, crabs required from 5 to 22 days to hatch most of their larvae (Fig. 5). Crab F1, which released the fewest larvae, also required the longest time (22 days) and was the last crab to finish hatching and extrude a new clutch. Although the minimum number of days required for hatching did not differ between groups, the maximum number of days required was 22, 13 and 8 for groups F, R and C, respectively. Consequently, the mean number of hatching days for group C (6.6) was significantly fewer than for group R (9.8) or group F (11.9 or 11.0 without crab F1), but the latter two did not differ significantly (MWU, $P = 0.412$, $n = 24$; Table 1). After crabs finished releasing their larvae, they stripped the empty egg cases from their pleopods immediately, and extruded a new clutch within 24 h.

Due to the fact that hatching occurred over a period of time, median dates (date on which 50% of total larvae had been released) were compared. The median

hatching dates for groups F, R and C were 15 May, 14 May and 18 May, respectively, and these did not differ significantly, with or without crab F1 (K–W test, Table 1). The overall median was 16 May (Fig. 6). Due to the fact that extrusion of new clutches occurred on a single day, mean dates were compared. The mean extrusion dates for groups F, R and C, respectively, were 19 May F, 17 May and 20 May, and these did not differ significantly (Table 1). Since actual hatching occurred the evening before larvae were counted, the median date of hatching for group C (from Chiniak Bay) coincided with the dates of tidal current reversal and the greatest tide exchange in May (Fig. 4). Cessation of mounding, and dispersal of crabs coincided with the end of hatching (Fig. 4).

Total number of larvae released by individual crabs ranged from 13,976 to 225,617 (Table 1). The largest number of larvae released in a 24 h period by one crab was 106,395. All crabs released 100% of their larvae except crab F1, which released only 84.1% (13,976 zoeae). The remaining 2640 were unhatched when they were stripped off the pleopods. Crabs in group F released significantly fewer larvae than groups R and C, which did not differ (Table 1). A multiple regression equation showed that the number of larvae was significantly dependent ($F = 20.91$, $P < 0.001$) on
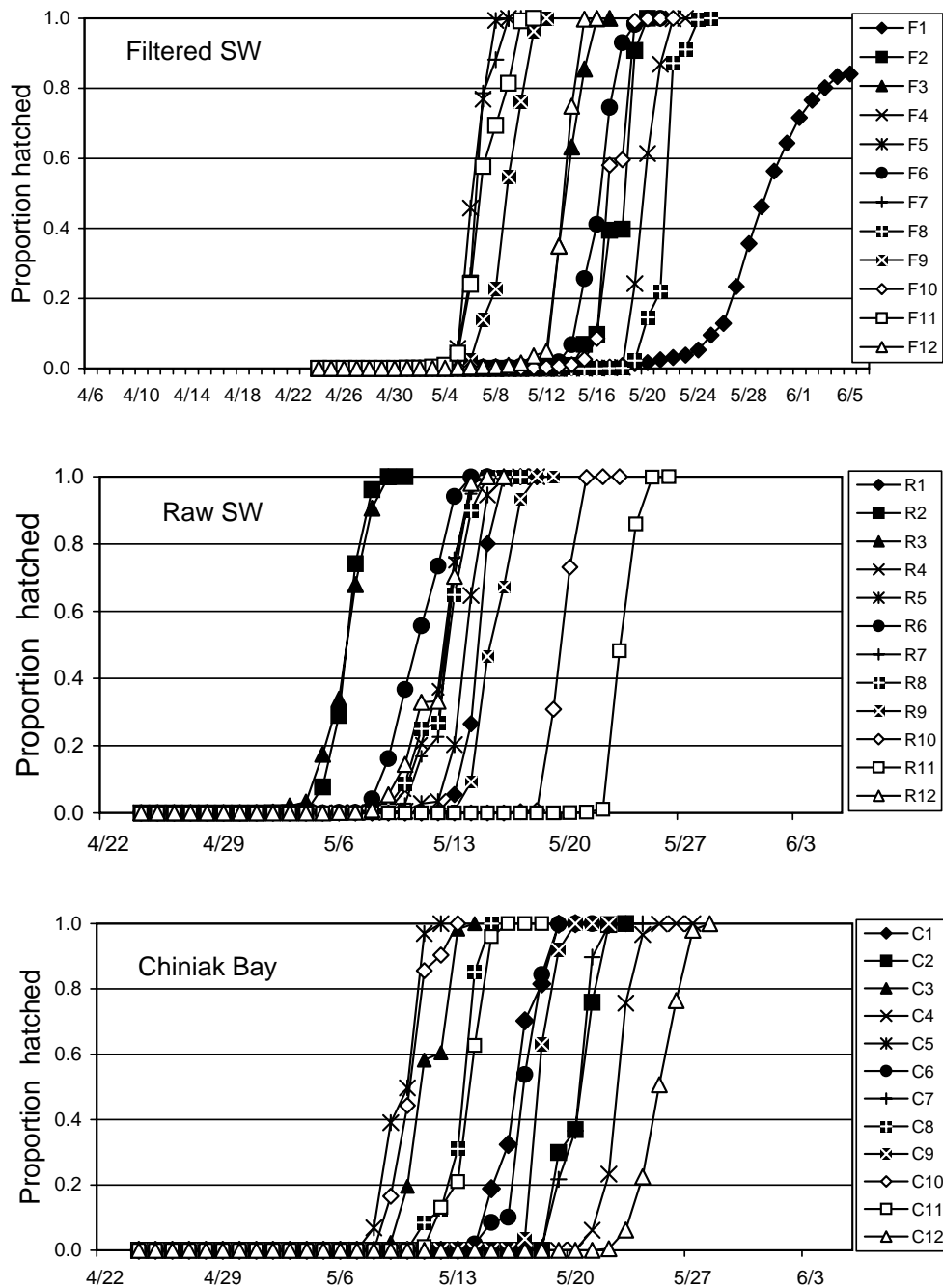
Fig. 5. Hatching trajectories for female Tanner crab. Data represent cumulative proportion of larvae released by each crab. Top two groups (filtered and raw) were collected from Kazakoff Bay by trawl on 4 April 1999. Crab F1 required the longest time and only released 84% of her larvae. Lower group was collected from mounds in Chiniak Bay by ROV.
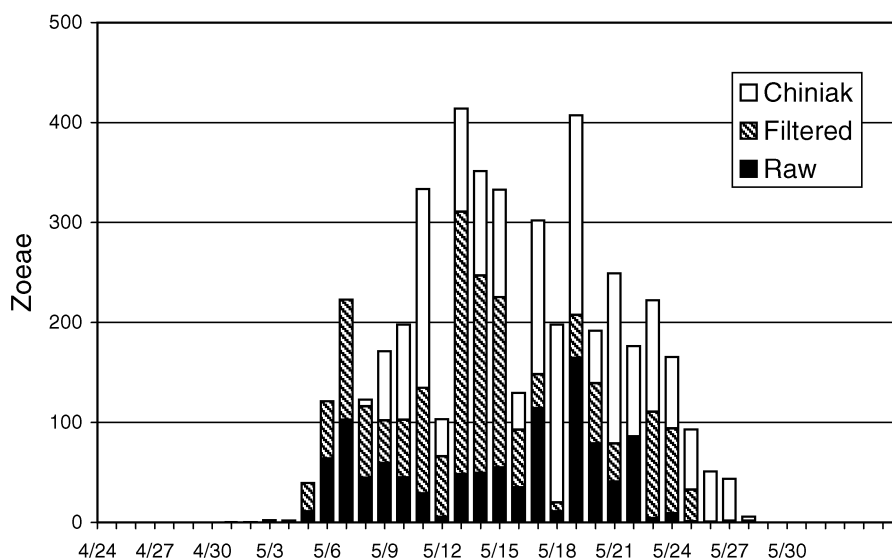
Fig. 6. Cumulative daily number of larvae released by female Tanner crabs in the three experimental groups. Each group contained 12 crabs.

both size and shell condition:

1000s of larvae

$$= -513.4 + 92.8 \times \text{shell} + 3.302 \times \text{CW},$$

$R^2 = 0.559$, $n = 35$

However, more realistic predictions can be made using regression equations for each shell condition category:

shell 3 (primiparous):

1000s of larvae $= 65.937 + 0.067 \times \text{CW}$,

$R^2 \leq 0.001$, $n = 9$

shell 4 (multiparous):

1000s of larvae $= -231.767 + 4.413 \times \text{CW}$,

$R^2 = 0.683$, $n = 25$

For nine shell 3 crabs, the regression equation was not significant, and the best estimate of larval release was the mean value of 72,173. The mean number of larvae released by 25 multiparous crabs (excluding F1) was 153,656. Predicted total numbers of larvae match the actual numbers released in groups R and C, but not in group F, due to the low output of crab F1 (Table 1).

In 2000, crabs in groups G and S began releasing larvae, or were already doing so, on the day of capture and finished within 3 days (Fig. 7); median dates of release were 1 and 2 May, respectively, 3–4 days prior to the high spring tide on 5 May. Crabs in group F and group R (which had been in the laboratory since April 1999) released larvae over a prolonged period, from 22 April to 31 May 2000. The three crabs that were monitored at 4 h intervals released 74.4% of their total larvae between 2000 and 0000 h, during the higher
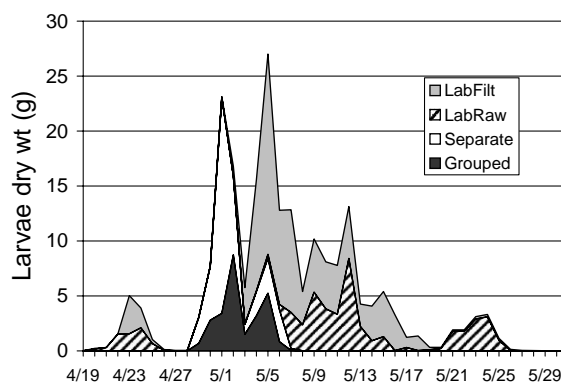

Fig. 7. Timing of larval release by female Tanner crabs in 2000. Recently captured crabs (separate and grouped) released all larvae within days of capture, whereas those that remained in the laboratory since spring 1999 released larvae over a prolonged period of 5 weeks.
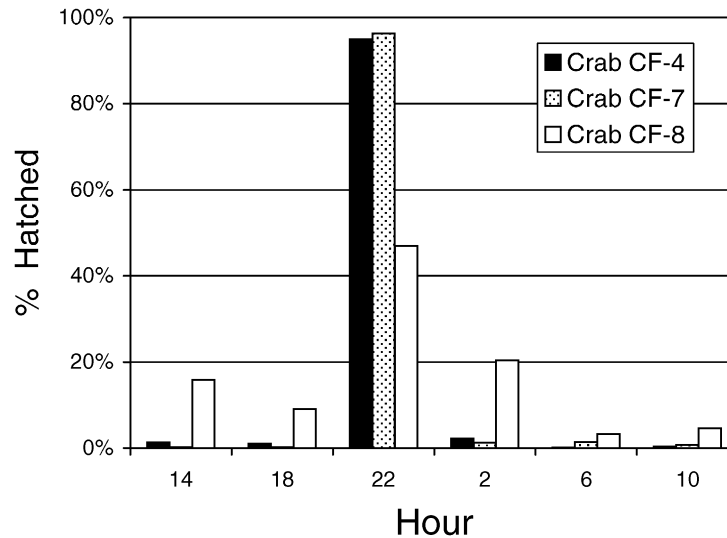
Fig. 8. Diurnal pattern of larval release by three female Tanner crabs in 4 h intervals. Two crabs released >95% of larvae between 2000 and 2400 h. Crab CF-8 released 48% in that interval and 30% within the previous or next interval.

low tide of the day (though two of the crabs released >95% of their larvae in that period) and 88.6% in the 12 h period between 1600 and 0400 h (Fig. 8). Sunrise and sunset occurred at 0507 and 2108 h on 6 May 2000.

4. Discussion

Data collected in 1999 are generally consistent with all four predictions of the "larval launch pad" hypothesis, but some modifications are required.

(1) Mound formation occurs coincident with local high spring tides.

In 1999, mounds began forming a month before the May spring tide and lasted for up to 6 weeks. A subjective "intensity" index reached a peak a week before hatching began and 2 weeks prior to the local high spring tides. Apparently larval release is coincident with spring tides, but mound formation must precede it.

(2) Local tides produce detectable changes in current patterns at the depths where the crabs occur.

Not only was there a 6 h tidal current pattern but also a complete reversal of the mean current at monthly intervals coinciding with spring tides.

(3) Mounds are associated with synchronous larval release.

Mounds began forming during the 18 April spring tide, but no significant numbers of larvae were released prior to 1 May. Tanner crabs in group C, captured from the study site, released their larvae during the few hours after dusk over a period of 18 days, although individual crabs required about 6 days. The median date of hatching coincided with the date of high spring tide in May, although hatching was not completed during the 3–4-day window of mean current reversal. Larval release did not coincide with the daily high tide. This hypothesis is further supported by the fact that crabs captured in 2000 released larvae within a few days of the high spring tide, even though it occurred 12 days earlier (6 May), as expected.

(4) Female crabs would form mounds when they were ready to release larvae, and would leave the mounds immediately after hatching was completed.

Crabs actually formed mounds up to a month ahead of larval release. However, crabs must have left the mounds after hatching, because the majority of female crabs recovered from mounds were preparing to release larvae, and a few were in the process of hatching. Very few post-hatch females

were captured from mounds. Mounds dissipated immediately after hatching had finished among laboratory held crabs. Occasional observations of hatching in the laboratory show that the female must be able to flap her abdomen to release the larvae. Thus, only crabs on the surface of the mounds could do so. Crabs beneath or inside the mounds could not be releasing larvae.

Once larvae start to hatch, they do so discontinuously, in short intervals after dusk, over a period of days to weeks. Without tidal influence, tidal synchrony is lost over time though larval hatching eventually occurs under some endogenous control. Thus, in contrast to the assertion by Starr et al. (1994) that snow crabs adapted to changing conditions by detecting the presence of phytoplankton, our data suggest that hatching of Tanner crab larvae is synchronised with tidal current patterns. Two aspects of our data, however, pose unanswered questions. First, how do the crabs (or larvae) select the high spring tide on which to hatch, because it is usually not the highest of the year (which occurs in July)? In some years, mound formation occurred on a HST in April, and in other years, in May (Stevens et al., 2000). One possibility is that a precursor signal may be required to "prime" the behavioural–physiological pathway leading to hatching. The primer signal may be phytoplankton-related, as suggested by Starr et al., but that alone does not appear to be sufficient to trigger hatching. The second unexplained observation is that crabs formed mounds several weeks before they began to release larvae in 1999. During the previous 6 years that we have observed mound formation, it usually has coincided with larval release, although 1999 produced the longest lasting mounds, and the latest hatching we have ever observed. This suggests that mound formation may occur when larvae are competent, or in response to some other stimulus, in anticipation of the tidal current signal that ultimately stimulates hatching, especially when the spring tide is later than usual.

The developing embryos may provide the primary trigger upon reaching competence for hatching. In the mud crab *Rhithropanopeus harrisii*, embryos release a "hatching hormone" that stimulates the mother crab to begin abdomen flapping behaviour and release the larvae (Rittschof et al., 1985; Forward et al., 1987). Occurrence of small numbers (<10) of Tanner crab larvae

in tanks for several days before massive larval release began suggests that the embryos were competent, and ready for hatching at that time. Such early "leakage" of embryos may occur when the environmental signals that stimulate the female to begin releasing the larvae are delayed beyond the point at which the embryos are ready to hatch. This may have been the case in 1999, when hatching occurred later than had previously been observed.

Virtually every species of crab that has been studied demonstrates rhythmic hatching behaviour in synchrony with some environmental variable (Forward, 1987). Most crabs from supralittoral environments have a semi-lunar hatching rhythm, releasing larvae on the new and/or full moons, usually at high tide. Those from littoral environments may release larvae in synchrony with high tides, whether it occurs during the full moon or some time afterwards (Christy, 1986; Forward, 1987). Crabs from subtidal environments generally release larvae at the onset of darkness (Forward, 1987), as does *C. bairdi*. At least one species, the mole crab *Emerita talpoida*, releases larvae following storm surge events (Amend and Shanks, 1999). However, most crabs in which hatching has been studied are shallow water, estuarine or subtropical species (Morgan, 1987; De Vries and Forward, 1989; Morgan and Christy, 1995; Palmer, 1997), including some semi-terrestrial forms (Saigusa, 1992, 2000). Most of these release all their larvae at one time, over a brief period, on 1 day. Many of these same species produce multiple broods during the summer, releasing subsequent broods at lunar or semi-lunar periods (Forward, 1987). Tanner crabs differ from this model, because they live in relatively deep oceanic water and release their larvae during multiple hatching events over extended periods of days to weeks. In this respect, they are similar to the lobster *Homarus gammarus*, which releases larvae in brief periods for a few minutes each evening over a period of several weeks (Ennis, 1973). That the rhythm in Tanner crabs is under endogenous control is evident from the fact that it occurs days to weeks after crabs are moved to the laboratory and once started, persists for many days. This rhythm is probably entrained by exposure to some environmental factor other than daylight or lunar cycles (that are negligible at their depth), or temperature or salinity changes, which are non-cyclic. Hatch timing of Tanner crab is probably not optimised

to avoid environmental stress, as suggested for *R. harisii* (Morgan, 1987). The most likely zeitgeber for such behaviour are physical factors associated with the spring tides. Forward (1987) has suggested that such rhythms could be entrained by hydrostatic pressure or mechanical agitation. For the Tanner crab, tidal current speed is equally likely.

If individual Tanner crabs released all their larvae in a single day, they might be expected to hatch in tighter synchrony with the tidal cycles. However, their extended hatching behaviour potentially explains why aggregations persist for weeks around the date of the spring tide. However, extended hatching, and loose synchrony, does not discredit the "larval launch pad" hypothesis. A hatching period of 12 days represents approximately 3.3% of the annual developmental period for Tanner crab. Estuarine crabs that release multiple broods at monthly intervals, and require only 1 day for hatching, utilise the same proportion of their developmental period for this process.

The observed data do not explain why female crabs form mounds. One possibility is that mounds of female crabs function as "larval launch pads" to elevate larvae up away from the silty bottom boundary layer when hatching, and thereby improve their chances of reaching the surface plankton layers and eventual survival. However, this study did not test that hypothesis, and there are no data to demonstrate that larval dispersal or survival is improved by such behaviour. Another possibility is that proximity of the crabs helps tighten the synchrony of hatching, perhaps by improving communication via pheromones or other chemical compounds released during hatching. This idea is currently under investigation.

One important ramification of tidally synchronised hatching is that it is decoupled from environmental indicators of food abundance. Due to the fact that the date of the HST advances predictably 11 days each year, hatching should advance by a similar offset, up to a date at which the larvae are not yet competent. This is supported by the hatching data for crabs collected in 2000. An important consequence is that linear changes in environmental parameters, such as temperature, do not necessarily result in linear changes in timing of larval release. Data collected during the annual NMFS eastern Bering Sea survey show that the proportion of female red king crab, *Paralithodes camtschaticus*, with eyed (unhatched) eggs is greater in years that

are colder than average, suggesting delayed hatching (Otto et al., 1989). Based on this information, Stevens (1990) developed a model of king crab recruitment that allowed the date of hatching to fluctuate by ±1 month depending on temperature. For the Tanner crab, our evidence suggests that changes in hatch timing occur in intervals of one lunar month, such that, if larvae are not developmentally ready to hatch on the HST in April, the next most acceptable hatching time would then be one lunar cycle (30 days) later. This implies that food abundance is not as important for larval survival as current patterns.

The timing of larval release has functional advantages for multiple reasons, one of which is reduced exposure to predators. According to Forward (1987), "...aggregation of larval releases into a small time interval would tend to swamp potential predators". That time interval can be 1 h in the day or 1 day in the month. An extension of this rule is that aggregation in space (as shown by Tanner crabs) would increase the larval concentration and swamping effect. Although the major predators of Tanner crab larvae are unknown, we have observed dense swarms of euphausids around crab mounds, so they might be likely predators.

Another potential benefit of tidally synchronised hatching would be the ability to take advantage of current patterns to deliver larvae to appropriate nursery areas. However, such currents are equally likely to increase dispersal away from the site of larval release. Current data for Chiniak Bay are unavailable for sites or depths other than the mooring we have used. The net current at 192 m is to the SW in Chiniak Bay. Data from drift buoys show that current patterns in nearshore waters of northeast Kodiak Island in late summer are circular, leading to long retention times. Surface currents move counterclockwise along shore in the northern Gulf of Alaska but offshore waters move swiftly to the west, along with the Alaska gyre (P. Stabeno, pers. commun.). Drifters released near Seward (480 km NE of Kodiak) travelled southwest to Kodiak and many ended up in Marmot Bay, just north of Chiniak Bay. Water masses moving into Shelikof Strait on the north side of Kodiak Island create a net SW current between islands of the Kodiak archipelago and into Chiniak Bay, with currents in some passes exceeding $8 \, \text{m} \cdot \text{s}^{-1}$. Although we did not measure surface currents, if similar to bottom currents, they would

carry larvae offshore, where the Alaska gyre would sweep them downstream to the open ocean. The reversed currents (to the NW) during high spring tides would tend to keep larvae inshore, possibly within Chiniak Bay, due to stable eddies.

Young-of-the-year Tanner crab are commonly observed in the shallow bays adjacent to Chiniak Bay, at depths of 12–20 m (personal observation, by scuba and small mesh trawl). We have rarely observed small crab in the area of the aggregation site. This suggests that nursery areas are inshore rather than offshore, or near the site of larval release. Thus, inshore water movement would be advantageous for larval survival, by transporting them to nursery areas. However, there is no data on depth preference or vertical migration patterns of Tanner crab larvae. Furthermore, the immediate benefits of tidally synchronous hatching would be extremely diluted by the long larval period of Tanner crabs (2 months or more in our laboratory).

The timing of larval release has a direct impact on their survival. According to the "match–mismatch" hypothesis (Hjort, 1914; Cushing, 1990), variability in larval survival occurs as a result of a mismatch between the fixed time of larval release and variable annual zooplankton production. An alternative "larval-retention" hypothesis (Sinclair and Tremblay, 1984) suggests that the time of metamorphosis from larva to juvenile (rather than hatching) is matched to the time of maximal food production. The "membership versus vagrancy" hypothesis (Fortier and Gagne, 1990) suggests that larval mortality is the result of advection from feeding areas, and that hatch timing is optimised to allow larvae to limit dispersal during critical early feeding stages. The latter hypothesis is probably most applicable to Tanner crab.

Female red king crabs (*P. camtschaticus*) return to specific areas for spawning in Auke Bay, Alaska (Stone et al., 1992, 1993). Studies with ultrasonic tags show that female king crabs spend the summer at depths of 50–80 m, then migrate to depths <30 m in the winter for moulting, during which they form pods similar in size and shape to those of Tanner crabs (Stevens et al., 1994). King crabs move to deeper areas in the spring for reproduction, when aggregations are more loosely knit (Stone et al., 1993). Mean depth was correlated with photoperiod, with crab staying below the thermocline. However, multiparous females moved very little. Their mean range was 3.6 km^2 (Stone et al.,

1992). The present study did not measure migration behaviour, but multiparous female Tanner crabs are rarely observed in shallow water <30 m (Stevens et al., 1993) and probably remain in the deeper parts of Chiniak Bay year-round.

Differences in fecundity between the three groups of crabs (F, R and C) can be accounted for by the significant multiple regression equation for shell and CW. However, more realistic predictions are obtained by using the regression for shell 4 crabs and the mean fecundity of shell 3 crabs. The latter were probably primiparous, carrying their first clutch, whereas shell 4 crabs were probably multiparous. Somerton and Meyers (1983) demonstrated that fecundity of primiparous crabs is, on average, 70% that of multiparous crabs. However, they estimated fecundity for females with new, uneyed eggs, whereas our data represent the actual number of larvae released. Our data show a greater disparity. An average sized female of 90 mm would release 72,000 larvae if primiparous, but 165,400 larvae if multiparous; more than a twofold increase in production. This disparity is probably due to the small sample size of nine primiparous crabs, but could also be due to greater egg loss or a lower proportion of fertilised eggs among primiparous crabs.

There was no apparent effect of filtered versus unfiltered water on hatching rates. Major differences occurred primarily between Kazakoff Bay crabs and Chiniak Bay crabs. Both groups F and R came from Kazakoff Bay and had been in captivity 25 days before any crab released 10 or more larvae. In contrast, crabs in group C began releasing small numbers of larvae within a few days of capture. It is possible that the length of time in captivity affected the timing of release. Those in captivity longer may have begun to lose synchrony with environmental stimuli more so than those that had been captured shortly before hatching. This is especially evident for those crabs that were held in the laboratory over a year and for released larvae in 2000. With or without crab F1, there were no major differences in the median hatch date, mean extrusion date or days required for hatching between Kazakoff Bay crabs maintained in filtered or unfiltered seawater.

In summary, the data show that female Tanner crabs form mounds prior to releasing larvae, that hatching occurs during the mounding period over a period of time centred around the high spring tide in May (although it occurs in April in some years), that crabs

leave mounds after hatching and that there is a detectable and distinctive tidal signal at the depths where this behaviour occurs. Larval release coincides with the onset of dusk, but it is not coincident with high tide. Mound formation and hatching did not correspond with any abrupt change in temperature or salinity or with the spring plankton bloom (as measured by Secchi disk readings), and there was no effect on hatch timing of raw versus filtered seawater. The data suggest that the timing of Tanner crab larval release is under the control of an endogenous biological clock and is optimised to match the period of greatest tidal exchange. Whether this corresponds with increased net transport towards inshore areas, or greater dispersal, remains to be seen. The fact that Tanner crab eggs develop over a period of 11 months and then hatch within 6–12 days is even more remarkable, and relatively more synchronous, than crabs that spawn monthly and hatch over 1–3 days.

Acknowledgements

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